# Antennal sensilla in adult males of five species of *Coleophora* (Coleophoridae): Considerations on their structure and function

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**Abstract.** A study of the antennae of five species of *Coleophora* Hübner, 1822 (Coleophoridae) has been carried out by scanning electron microscope in order to determine the morphological types of sensilla and to compare these results with those obtained for *C. obducta* (Meyrick). In adult males, eight types of sensilla were observed on the flagellum: uniporous sensilla chaetica, multiporous sensilla trichodea, three types of multiporous sensilla basiconica, multiporous sensilla coeloconica, aporous sensilla styloconica and aporous sensilla squamiformia. In view of their morphology, sensilla chaetica are contact chemoreceptors, sensilla squamiformia are tactile mechanoreceptors, sensilla styloconica are thermo-hygroreceptors, and sensilla trichodea, basiconica and coeloconica are olfactive chemoreceptors. No sensilla placodea have been observed. These results differ partially from those previously described for *C. obducta* in regards to the interpretation of the structure and function of some sensilla.

**Résumé.** L'étude des antennes de cinq espèces du genre *Coleophora* Hübner, 1822 (Coleophoridae) a été réalisée au microscope électronique à balayage afin de déterminer les types morphologiques de sensilles et de comparer ces résultats à ceux obtenus chez une autre espèce. Chez les mâles adultes, il y a huit types de sensilles sur le flagelle: des sensilles chétiformes à pore unique, des sensilles trichoïdes multipores, trois types de sensilles basiconiques multipores, des sensilles coeloconiques multipores, des sensilles styloconiques sans pore et des sensilles squamiformes sans pore. D'après leur morphologie, les sensilles chétiformes sont des chimiorécepteurs de contact et les sensilles squamiformes sont des mécanorécepteurs tactiles, les sensilles styloconiques sont des thermo-hygrorécepteurs, les sensilles trichoïdes, basiconiques et coeloconiques sont des chimiorécepteurs olfactifs. Aucune sensille placoïde n'a été observée. Nos résultats diffèrent partiellement de ceux décrits antérieurement chez *C. obducta* en ce qui concerne l'interprétation de la structure et de la fonction de certaines sensilles.

## Introduction

Yang et al. (2009) describe nine types of sensilla (s.) from the antennae of *Coleophora obducta* (Meyrick, 1931), an important defoliator of larch in northeast China: s. placodea, s. basiconica, s. coeloconica, s. styloconica, s. trichodea, s. squamiformia, s. furcatea, terminal sensory pegs and Bohm's bristles. While most of these sensilla are recognised in Lepidoptera, the s. placodea occur only in Micropterigidae (Faucheux 1997, 2004) and the s. furcatea have so far not been observed in Lepidoptera (Faucheux 1999, Hallberg et al. 2003). Consequently, the presence of these structures needs to be confirmed in species other than *C. obducta*. Moreover, according to Yang et al., the s. styloconica are regarded as gustatory/mechanosensory receptors, which contradicts all contemporary views which attribute a thermo-hygroreceptive function to the s. styloconica found on antennae of adult lepidopterans (e.g. Hallberg et al. 2003). These results prompted me to examine the sensory equipment of the antennal flagellum of several additional species of *Coleophora* by scanning electron microscopy in order to note the sensillum types and to compare them with those described by Yang et al. The results of the present investigation will be discussed together with the interpretations concerning *C. obducta*.

## Material and methods

Material. *Coleophora pennella* (Denis & Schiffermüller, 1775): 1 ♂, France, Sainte Emilienne, Olonne sur mer, Vendée, 02/03.VI.2001, Drouet leg. – *C. fuscicornis* (Zeller, 1847) 1 ♂, France, Chemin du Seyran, Draguignan, Var, 24.IV.2006, Drouet leg. – *C. lixella* (Zeller, 1849) 1 ♂, France, Saint Generoux, Deux Sèvres, 07.VI.2008, Drouet leg. – *C. frischella* (Linnaeus, 1758) 1 ♂, France, Port de la Guittière, Talmont, Vendée, 28/29.VII.2002, Drouet leg. – *C. albella* (Thunberg, 1788) 1 ♂, France, Port-au-duc, Saint Fiacre sur Maine, Loire-Atlantique, 08/09.V.2002, Drouet leg.

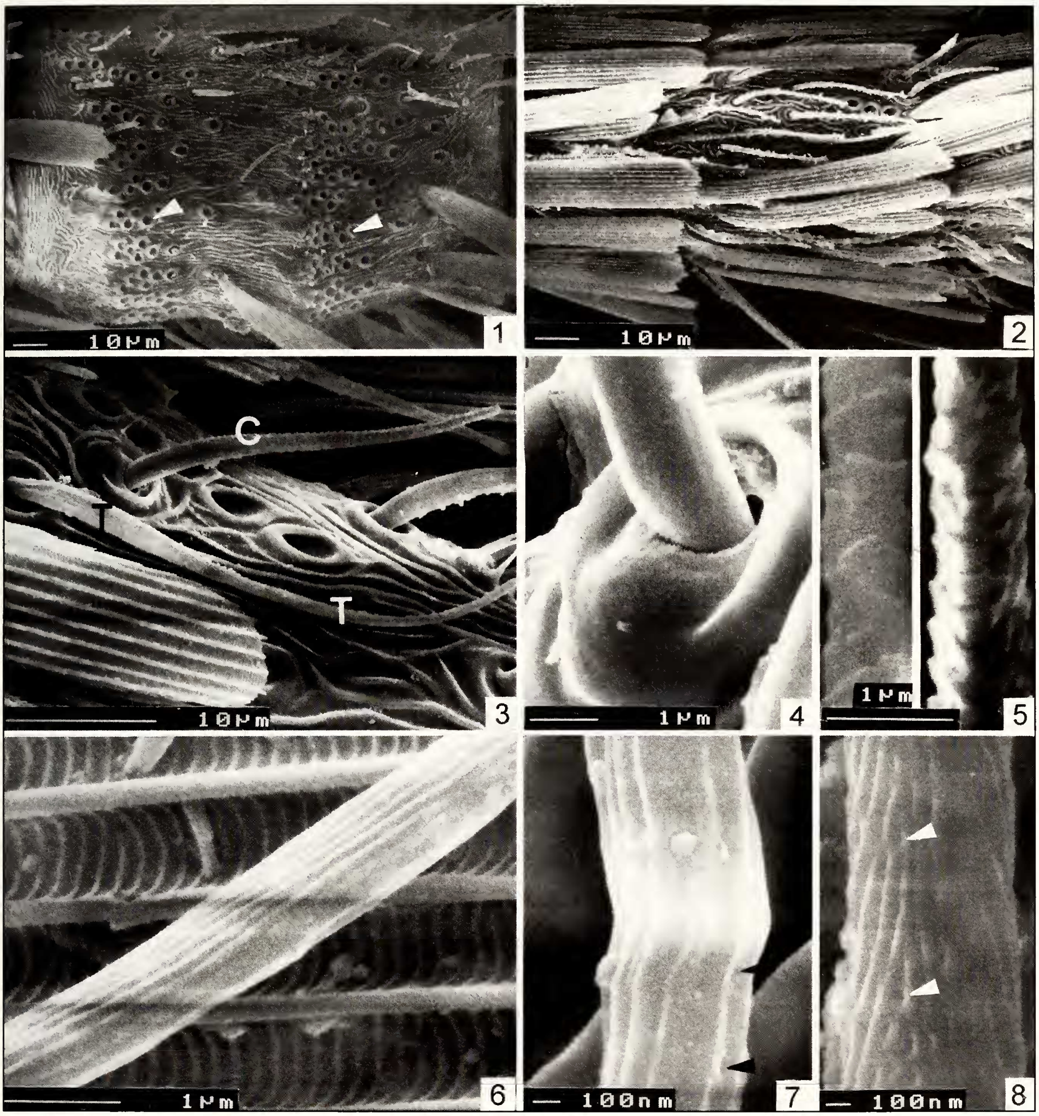
The five males examined were dry insects from Eric Drouet's collections. For SEM study, the antennae of each moth were cleaned in acetone, dehydrated into pure alcohol and mounted, one on the ventral and one on the dorsal face, on specimen holders. After coating with gold and palladium, preparations were examined in a Jeol J.S.M.6400 F SEM at 10 kV. Sensilla terminology follows Faucheux (1999) and Hallberg et al. (2003).

## Results

The male antenna of all *Coleophora* species reaches to about the middle of the forewing costa. It consist of a large scape, a pedicel and a filiform flagellum composed on average of 24–30 flagellomeres in which the length is greater than the width. The dorsal and ventral surfaces of the flagellum have appressed lamellar scales. The sockets of most scales are grouped in two rings on each flagellomere: one subproximal ring and one subdistal ring (Fig. 1). Each ring is made up of some twenty roughly longitudinal rows of 3–6 scales each. A few rare scales are scattered between the two rings and in the distal region of the flagellomere. As a result of this arrangement, the scales of the two rings partially overlap. A window without scales is usually located on the ventral face of each flagellomere (Fig. 2). The integument of the flagellum is devoid of microtrichia but shows sinuous and clearly visible folds arranged longitudinally, and closely grouped together side by side (Figs 1, 3, 13).

The sensory structures of the flagellum comprise eight types of sensilla: uniporous s. chaetica, multiporous s. trichodea, multiporous s. basiconica types 1, 2 and 3, multiporous s. coeloconica, aporous s. styloconica, and aporous s. squamiformia. With few exceptions, no significant differences were observed between the five species regarding the morphological types and the number of sensilla.

Uniporous sensilla chaetica are long sensilla (range 24.7–28.3 µm); their diameter decreases steadily from base (1.5 µm) to apex (0.7 µm) (Fig. 3). They articulate into a basal cupola, which restricts the movement of the hair (Fig. 4). The latter is adorned with deep transverse furrows sometimes accompanied by a few longitudinal ridges (Fig. 5); this structure gives a ringed aspect to the hair. The blunt apex is pierced by a hardly visible pore (even with SEM). Unlike the other sensilla, which are more or




**Figs 1–8.** Antennal sensilla of *Coleophora* spp. **1.** Descaled dorsal surface of 13th flagellomere of *C. albella*. Arrowheads indicate the scale sockets. **2.** Area without scales on the ventral surface of 17th flagellomere in *C. frischella*. **3.** Uniporous sensillum chaeticum (C) and multiporous sensillum trichodeum (T) in *C. fuscicornis*. **4.** Base of sensillum chaeticum in *C. fuscicornis*. **5.** Two aspects of the wall of sensillum chaeticum in *C. fuscicornis*. **6.** Middle part of sensillum trichodeum in *C. fuscicornis*. **7.** Detail of sensillum trichodeum in *C. pennella* showing some pores (arrowheads). **8.** Lined pores of type 1 multiporous sensillum basiconicum (arrowheads) in *C. albella*.

less flattened against the antennal integument, s. chaetica are perpendicular to it or obliquely directed towards the antennal apex and are therefore the only ones to emerge between the scales. As a result, they can more readily make contact with the surrounding medium. They are evenly distributed and number from 4 to 6 per flagellomere.

Multiporous sensilla trichodea are the longest (range 34.2–39.7 µm) and the slenderest of all antennal sensilla (T, Fig. 3). Their diameter varies from 1.8 µm at the base

**Table 1.** Types of flagellar sensilla (s.) in *C. obducta* (Yang et al. 2009) and their reinterpretation based on the five other species of *Coleophora* examined in this study.

| ***Coleophora obducta*** | ***Coleophora* spp. (5 species)** |
|---|---|
| s. basiconica | uniporous s. chaetica |
| s. placodea | multiporous s. trichodea |
| s. trichodea | multiporous s. basiconica 1 |
| not described | multiporous s. basiconica 2 |
| not described | multiporous s. basiconica 3 |
| s. coeloconica | multiporous s. coeloconica |
| s. styloconica | aporous s. styloconica |
| s. squamiformia | aporous s. squamiformia |
| s. furcatea | not described |
| terminal sensory pegs | not described |

to 0.9 µm at the apex. They are curved and often found in areas without many scales on each flagellomere (Fig. 2). The hair possesses longitudinal ridges which are present over the whole length (Fig. 6); the pores are visible in Fig. 7 and the pore density was estimated at 25 pores/µm$^2$. The number of sensilla is about 10–15 per flagellomere in the five species.

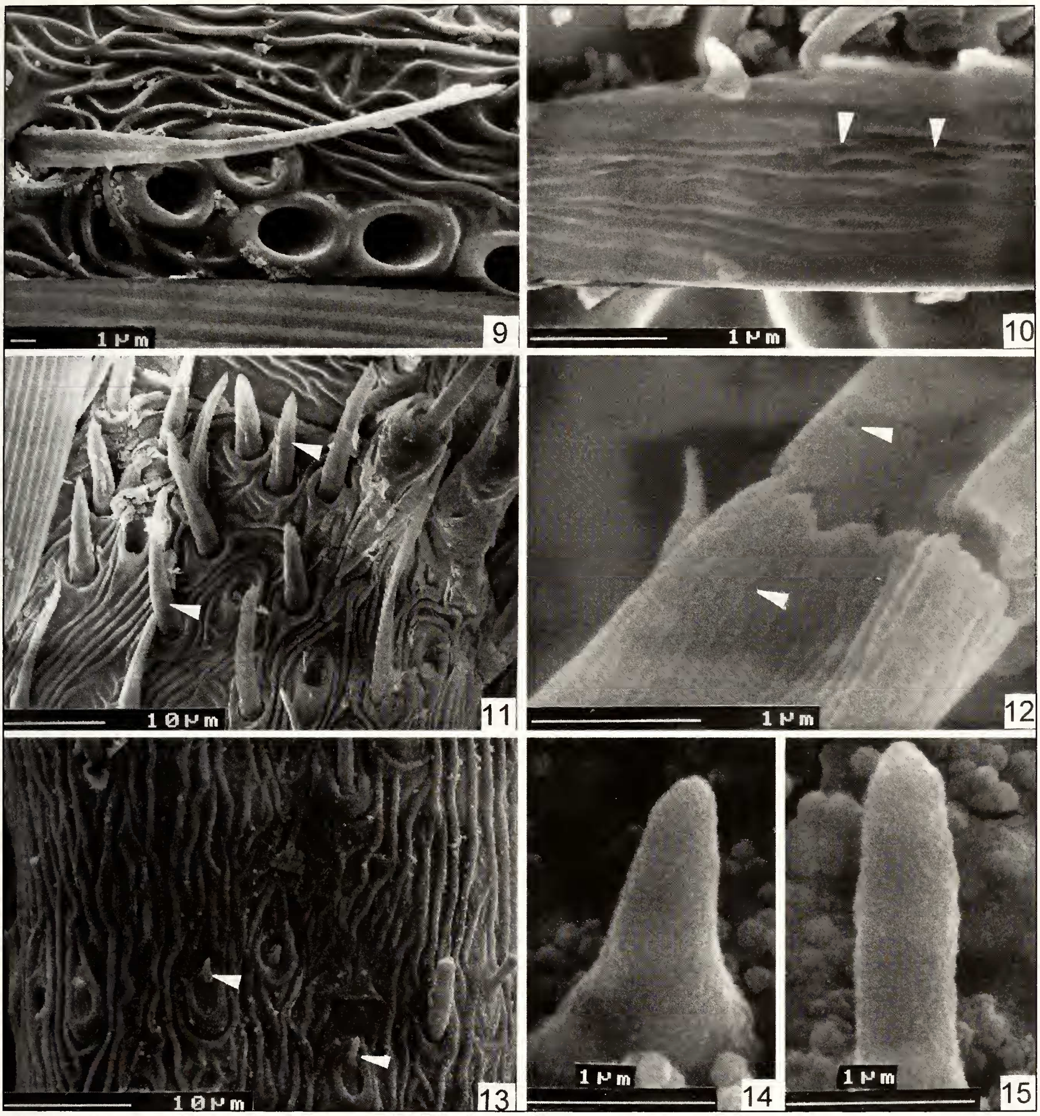
Multiporous sensilla basiconica type 1 are of similar length to that of the s. chaetica (range 19.1–26.5 µm) but differ by the absence of a cupola and the presence of wall pores (Figs 8–10). The proximal half of the hair is frequently flattened and adorned with barely visible pores (Fig. 10) whereas the distal half is more cylindrical and provided with pores arranged into longitudinal or oblique rows with a pore density of 53/µm$^2$ (Fig. 8). The maximum number of sensilla is 3–4 per flagellomere.

Multiporous sensilla basiconica type 2 are easily recognisable by their small size (length range 8.7–13.4 µm) and by the fact that they are grouped by 12 to 15 sensilla in the distal region of the flagellomere (Fig. 11). They are frequently flattened and in that case resemble s. auricillica. Their pores are arranged in longitudinal rows over the whole sensillum (Fig. 12). The thinness of the wall is visible on the break of the sensillum in Fig. 12. The pore density is 32/µm$^2$.

Multiporous sensilla basiconica type 3 are the smallest of the s. basiconica (range 1.5–2.4 µm) and have only been observed in *C. frischella*. With the usual technique for the preparation of samples for SEM work, the pores are invisible. The sensilla are located on the ventral face of the antenna in zones with large unscaled areas (Fig. 13). They take the form of a cone or a peg occupying a pit in the integument limited by a thick ridge (Figs 13, 14, 15).

Multiporous sensilla coeloconica are composed of a longitudinally grooved cone, 4.5 µm long, surrounded by a cuticular fringe of 13–15 microtrichia (Fig. 16). In the majority of species, they are mostly found latero-distally on each flagellomere and number 2–3 per flagellomere.

Aporous sensilla styloconica with a stylus of 21.5–25.8 µm in length are found on the lateral face of each flagellomere except for the basal and apical one (Fig. 17),




**Figs 9–15.** Antennal sensilla of *Coleophora* spp. 9. Multiporous sensillum basiconicum of type 1 in *C. fuscicornis*. **10.** Detail of lined pores in the same (arrowheads) **11.** Multiporous s. basiconica of type 2 in *C. albella* (arrowheads). **12.** Detail of lined pores (arrowheads). **13.** Multiporous s. basiconica of type 3 in *C. frischella* (arrowheads). **14, 15.** Detail of the preceding sensilla.

towards the distal end of the flagellomere. The cone without pore measures on average 3.5 μm (Fig. 18). There is only one sensillum per flagellomere.

Aporous sensilla squamiformia resemble lamellar scales but differ in their shorter length (30 μm versus 70 μm), and in their slender distal end (Fig. 19). Their ornamentation is similar to those of the scales (Fig. 20). They are rare, from 1 to 2 per flagellomere, with numerous flagellomeres without any.

## Discussion

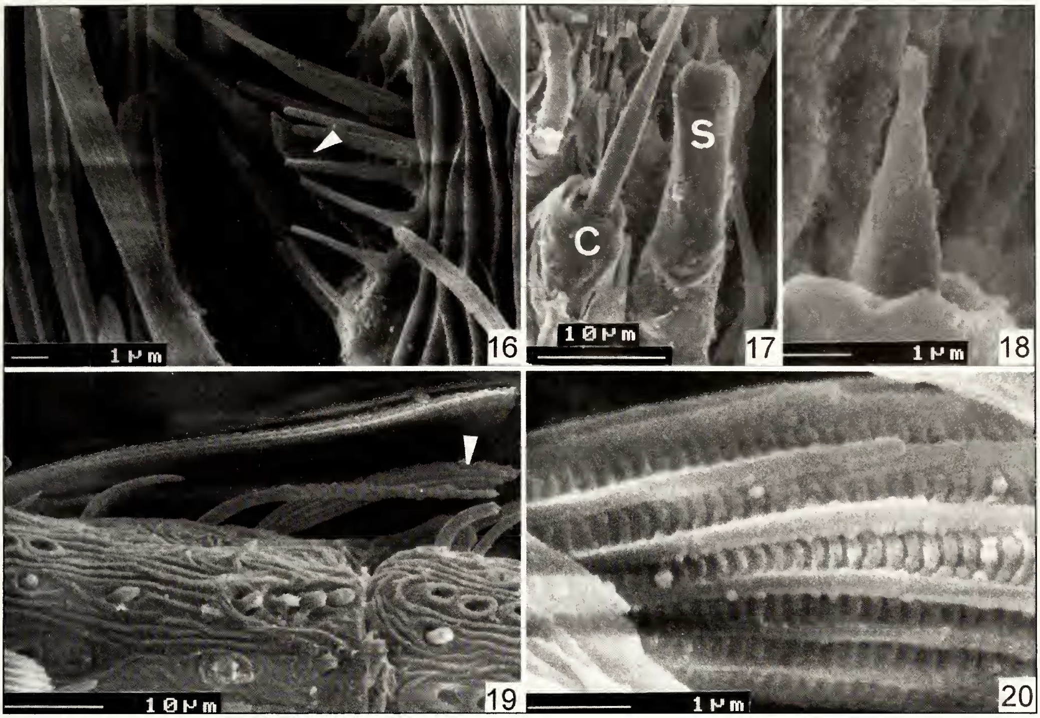
The antennae of the five examined *Coleophora* species possess the majority of the ubiquitous sensilla of Lepidoptera. Except for the s. trichodea, the other morphological types have common characteristics shared with all Lepidoptera. With the s. trichodea, those described so far show a ridge pattern that is helical at the base and more annular over the remaining length of the sensillum. Pores are located in the depressions between the ridges (Cuperus 1983, 1985; Faucheux 1999). On the contrary, in the five checked species of *Coleophora*, the sensilla show a longitudinal ridge pattern and pores arranged in longitudinal rows. However, a common characteristic is shared by the s. trichodea of *Coleophora* and those of other Lepidoptera species: their low pore density compared with that of s. basiconica (Steinbrecht 1973, Shields & Hildebrand 1999).

These results differ from those obtained by Yang et al. (2009) in *C. obducta* regarding the interpretation of the morphological types and their function (Table 1). The multiporous s. trichodea correspond to the alleged "sensilla placodea" of *C. obducta*. Indeed, like the latter, they represent the most extensively distributed type of male sensilla; they are generally curved and show the "characteristic pattern of vertical veins" described by Yang et al. (2009). The low magnification used by the authors made it impossible to observe the wall pores. The term "placodea" is inadequate because, by definition, this type is not hair-shaped but has the shape of a plate fixed by its base to the integumental surface and it is pierced by numerous pores. In Lepidoptera, s. placodea occur only in Micropterigidae (Faucheux 1997, 2004). Since the s. trichodea possess no terminal pore but only wall pores, and since wall-pore sensilla usually have an olfactory function, while the contact-chemoreceptory function appears to be limited to sensilla having pore only on their apex (Altner & Prillinger 1980, Hallberg et al. 2003), the hypothesis of contact-chemoreception in *C. obducta* advanced by Yang et al. (2009) cannot be confirmed. The large number of s. trichodea compared to other antennal sensilla observed in *C. obducta* and the five species from this study suggests a pheromone chemo-reception for these sensilla in males.

The multiporous s. basiconica type 1 resemble the "sensilla trichodea" of *C. obducta* in Yang et al. (2009). Although the pores are not mentioned, Yang et al. (2009: 235, fig. 6b) suggest their presence. These sensilla are olfactory receptors (Hallberg et al. 2003).

The uniporous s. chaetica are the "sensilla basiconica" of *C. obducta* in Yang et al. (2009). Yang et al.'s fig. 3e (2009: 233) is characteristic of s. chaetica with a terminal pore because of the existence of a thick wall (confused with the sensilla lymph lumen), and a cavity occupied by dendrites; moreover, the authors do not report the presence of wall pores. Functions attributed to the s. basiconica of other insect species, and in particular the "detection of related chemical compounds that constitute the plant fingerprint" (Yang et al. 2009) are unlikely to apply to these sensilla. Based on their similarity to morphologically characterized uniporous s. chaetica of other Lepidoptera, the s. chaetica of *Coleophora* are probably contact chemoreceptors.

The multiporous s. basiconica of type 2 and 3 are not described in *C. obducta* by Yang et al. (2009). The s. basiconica type 2, which have a cuticular wall that is thin




**Figs 16–20.** Antennal sensilla of *Coleophora* spp. **16.** Multiporous sensillum coeloconicum (arrowhead) in *C. lixella*. **17.** Aporous sensillum styloconicum (S) and uniporous s. chaeticum (C) in *C. albella*. **18.** Cone of sensillum styloconicum. **19, 20.** general view and detail of aporous sensillum squamiformium in *C. pennella*.

and pierced by numerous pores, may be considered to be the main receptors for plant volatiles (Den Otter et al. 1980, Lopes et al. 2002). A similar function is also possible for the s. basiconica type 3.

The multiporous s. coeloconica with a fringe of microtrichia have been observed in the five species studied while only the "naked" type is described in *C. obducta* by Yang et al. (2009). Their function is olfactive (Den Otter et al. 1978, Pophof 1997). In *Bombyx mori* (L.) the neurons of these sensilla are excited by some short-chain aliphatic acids and aldehydes and inhibited by some monoterpene alcohols; they do not respond to the moth's pheromones, and they may be involved in choosing oviposition sites (Pophof 1997, Hunger & Steinbrecht 1998).

Aporous s. styloconica are thermo-hygroreceptors in moths (Gödde & Haug 1990, Steinbrecht & Müller 1991, Steinbrecht 1998). Yang et al. (2009) attribute a combined gustatory/mechanosensory function to the s. styloconica of *C. obducta*. But this function supposes the presence of a terminal pore (Altner & Prillinger 1980) which is not described in this species. Moreover, Yang et al.'s fig. 5f (2009: 234), which is supposed to represent a tubular body characteristic of mechanoreceptors, is by no means demonstrative. While a terminal sensory pore is observed in the uniporous s. styloconica of the galeae of moths, all previous studies have revealed its absence in the antennal s. styloconica of Lepidoptera (Faucheux 1999, Hallberg et al. 2003). The apical pore found on the s. styloconica of the antennae of some adult lepidopterans appears to be a moulting pore (Haug 1985), and there is no evidence that this kind of pore may transmit external stimuli to the sensory cells (Altner et al. 1983).

Aporous s. squamiformia resemble s. squamiformia present in *C. obducta*. A sole sensory neuron with a tubular body at the base of sensillum is described in these sensilla (Schneider & Kaissling 1957, Schneider 1964). S. squamiformia are involved in tactile mechanoreception (Faucheux 1999).

Most likely the s. furcatea in *C. obducta* as recorded by Yang et al. (2009) are only anomaly form of a sensillum basiconicum. Such anomalies are rare; in moths, they occur in the s. basiconica of *Monopis crocicapitella* (Clemens, 1859) (Tineidae) (Faucheux 1987) and the s. auricillica of *Pieris rapae* (Linnaeus, 1758) (Pieridae) (Faucheux 1996).

The existence of "terminal sensory pegs" in *C. obducta* is by no means confirmed by Yang et al. (2009: 236, fig. 10), and therefore currently their existence must be viewed as hypothetical.

In conclusion, the antennal sensory equipment of *Coleophora* species is typical for that of other Lepidoptera. The present study shows the need to carry out active research on the presence of pores, even if the latter are sometimes difficult to observe with SEM.

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